Growth and abundance of Pacific sand lance, *Ammodytes hexapterus*, under differing oceanographic regimes

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Synopsis

Dramatic changes in seabird and marine mammal stocks in the Gulf of Alaska have been linked to shifts in abundance and composition of forage fish stocks over the past 20 years. The relative value (e.g., size and condition of individual fish, abundance) of specific forage fish stocks to predators under temporally changing oceanographic regimes is also expected to vary. We inferred potential temporal responses in abundance, growth, and age structure of a key forage fish, sand lance, by studying across spatially different oceanographic regimes. Marked meso-scale differences in abundance, growth, and mortality existed in conjunction with these differing regimes. Growth rate within stocks (between years) was positively correlated with temperature. However, this relationship did not exist among stocks (locations) and differing growth rates were better correlated to marine productivity. Sand lance were least abundant and grew slowest at the warmest site (Chisik Island), an area of limited habitat and low food abundance. Abundance and growth of juvenile sand lance was highest at the coolest site (Barren Islands), an area of highly productive upwelled waters. Sand lance at two sites located oceanographically between the Barren Islands and Chisik Island (inner- and outer-Kachemak Bay) displayed correspondingly intermediate abundance and growth. Resident predators at these sites are presented with markedly different numbers and quality of this key prey species. Our results suggest that at the decadal scale, Gulf of Alaska forage fish such as sand lance are probably more profoundly affected by changes in abundance and quality of their planktonic food, than by temperature alone.

Introduction

Pelagic fishes are often subject to large-scale fluctuations in productivity thought to relate to oceanographic variability (Dragesund et al. 1997, Francis et al. 1998). Causal links between oceanic processes and fish are often difficult to disentangle. Most studies have used correlation between time series of stock states in attempts to link physical processes with fish productivity (Francis et al. 1998). An alternative strategy is to study biological processes across physical regimes, which may vary spatially. Lower Cook Inlet in the Gulf of Alaska (Figure 1) provides the opportunity to study a key semi-pelagic fish, sand lance (genus *Ammodytes*), under very different oceanographic conditions (Trasky et al. 1977).

Sand lance are ubiquitous in boreo-arctic coastal regions of the North Atlantic and North Pacific. Within this area sand lance constitute a key prey species for many vertebrate predators including seabirds, fishes, and marine mammals (Field 1988, Willson et al. 1999). *Ammodytes hexapterus* is the only sand lance species
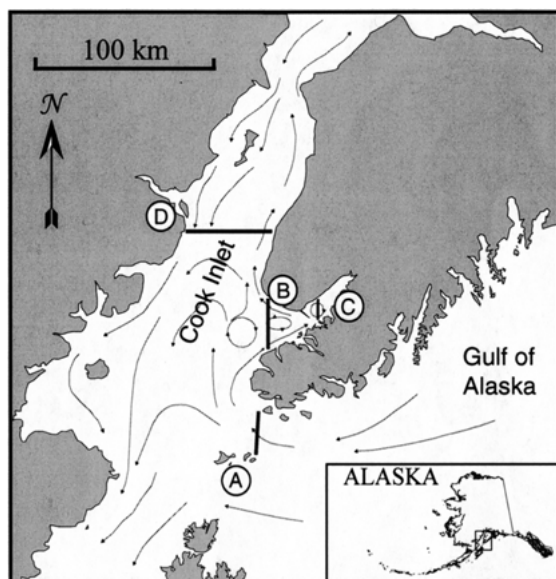
Figure 1. Location of study sites in Lower Cook Inlet showing the prevailing currents (based on Trasky et al. 1977). Study sites are A – Barren Islands, B – outer-Kachemak Bay, C – inner-Kachemak Bay, D – Chisik Island. CTD transects are shown as dark lines.

known to occur in the northeastern Pacific (Field 1988). However, despite their importance in the food web and the growing interest in modeling ecological processes (Chambers & Miller 1995), little is known about *A. hexapterus* age structure, growth, relative abundance, or how environmental processes influence these parameters. Differences in quality, size, and abundance of sand lance among areas would present local predators with markedly different potential returns. This may be particularly important for species such as seabirds that carry a limited number of prey items back to their nestlings.

Growth is dependent on both abiotic and biotic factors such as temperature, food availability, competition, and predation (Nelson & Ross 1991). As a result, stocks inhabiting different oceanographic regimes may exhibit differing growth and survival rates. In this paper, we investigate the relative importance to growth and survival of an abiotic factor (temperature) in comparison to a biotic factor (food availability). Growth comparisons between different sand lance stocks at a standard age were made using back-calculations from sand lance otoliths. Therefore, we also contribute the first published relation between otolith size and *A. hexapterus* length, and provide validation for timing

of annulus formation. We investigate age and regional differences in the somatic-otolith relationship in relation to local oceanographic regimes, and discuss the degree of potential error for trophic studies that assign single regressions covering several distinct stocks.

Oceanographic setting

The Alaska Coastal Current passes north of the Barren Islands, leading to intense upwelling of cold, nutrient-rich waters onto the shallow shelf of southeast Cook Inlet (Burbank 1977). The well-mixed nutrient-rich water passes into outer-Kachemak Bay and subsequently past the 7 km Homer Spit into the more estuarine inner-Kachemak Bay interrupted by two semipermanent gyres (Trasky et al. 1977). The gyre system acts to increase the residence time of water in outer-Kachemak Bay and contributes to the early development of a large spring and summer plankton stock (Feder & Jewett 1987). Water exits along the north side of Kachemak Bay before circulating in a counter clockwise direction within Cook Inlet and past Chisik Island (Figure 1). Waters are warmest and most estuarine around Chisik Island, having received significant glacier-fed freshwater input from large rivers at the head of Cook Inlet (Burbank 1977, Feely & Massoth 1982) and from the adjacent glacially-fed bay to the west. The highly turbid estuarine water around Chisik Island supports low chlorophyll-a concentrations, with one-tenth the productivity found elsewhere in Cook Inlet (Larrance et al. 1977, Feder & Jewett 1987).

Materials and methods

Oceanographic parameters

The most detailed descriptions of local oceanography (Larrance et al. 1977, Damkaer 1977, Feder & Jewett 1987) were published over a decade ago. Although we were unable to conduct a concurrent multi-year seasonal investigation of oceanography and productivity at all sites, we collected sea surface temperatures (SSTs); and conductivity, temperature, and density (CTD) profiles to establish if the previously described patterns of oceanography within Cook Inlet were consistent with current conditions. Nearshore water temperatures were measured at 10 min intervals with temperature loggers (Optic StowAway version 2.02,

Onset Computer Corporation). Loggers were placed at 3 m below low water (0 m) in inner-Kachemak Bay (permanent placement) and at outer-Kachemak Bay, Chisik Island, and the Barren Islands (July only). A (CTD) recorder (Seabird Electronics Inc, SBE-19 SEACAT profiler) was used to collect vertical temperature and salinity profiles along a transect adjacent to each study site (Figure 1) during July 1997.

Sand lance sampling strategy

Fish were collected by beach seine and random digging in intertidal substrates (Table 1). Beach seine construction was of knotless nylon stretch-mesh. Dimensions of the seine were 44 m long, with a 4 m deep, 3 mm mesh in the middle 15.3 m section, tapered to 2.3 m deep with 13 mm mesh in the wings. The net was set parallel to shore at a distance of 25 m as described by Cailliet et al. (1986). Inner-Kachemak Bay was sampled approximately every two weeks from May to September and once per month through the winter during 1996 and 1997. The other Cook Inlet sites were sampled approximately every two weeks from late June until September during 1996 and 1997.

All sand lance caught in seines were measured unless catches were large; in these cases an 8-liter sub-sample was collected from each haul. Sand lance collected from exposed substrates were less numerous, therefore, all individuals were retained for measuring. Stratified samples (5-mm size classes, 15 fish per class) were collected each month to develop seasonal age/length keys. Based on our small size classes and reasonable sample size this method was expected to produce reliable length estimates (Macdonald 1987, Devries & Frie 1996). However, adult sand lance were only sporadically caught in seines (Robards et al. 1999a) and

only available in intertidal substrates on infrequent negative-tides. This precluded the comparison of size-at-age between stocks for specific time periods. Therefore, to allow inter-area comparisons, we calculated size at end of the annual growing season via otolith interpretations. Samples of sand lance otoliths were collected between July and September 1997 (post-annulus formation; see otolith validation) from all sites to allow length-at-age and growth curves to be calculated. All sand lance were immediately measured to fork length (mm), blotted dry, weighed (±0.01 g), individually bagged, and frozen. No significant gender differences exist for mean length at age of *A. hexapterus* (Robards et al. 1999b) or *A. dubius* (North Atlantic, Nelson & Ross 1991), thus age data for each sex were combined for growth analyses.

Otolith protocol

In response to frequent requests for validation of otolith methodology (e.g., Devries & Frie 1996) we have included these results within our methods. Sagittal otoliths were removed, cleaned of fibrous material, bonded to microscope slides using crystalbond thermal resin, and aged on two separate occasions. Otoliths from all age classes of sand lance had clearly defined bands and only 12 of the 3909 otoliths (<1%) provided inconsistent readings or were unreadable due to indistinct ring formation. Age designations are based on a 1 January hatching date (Dick & Warner 1982, Robards et al. 1999b), with first year sand lance designated as group-0, second year as group-1, up to seventh year (group-6). The terms juvenile and adult are used to describe group-0, and group-1 or older respectively.

Total and within-annulus areas, as well as annular diameters were measured using a video imaging system

Table 1. Catch statistics for sand lance collected in Lower Cook Inlet during 1996 and 1997.

	Chisik Island (Jun–Sep)	Inner-Kachemak (Jun–Sep)	Inner-Kachemak (Oct–May)	Outer-Kachemak (Jun–Sep)	Barren Islands (Jun–Sep)
Number of beach seines	48	341	170	49	68
Sand lance collected in seines	328	170 159	6694	6713	188 660
Number of digs	9	49	15	0	0
Sand lance collected in digs	359	2483	875	0	0
Otoliths used for age lg^{-1} keys	284	1622	1183	669	151

Table 2. Relationship between root otolith area and fork-length for sand lance collected at the different sites. Relationship is expressed as: fork length = (a·root otolith area) + b.

Location	Interval	n	a	b	r^2	r^2 for otolith diameter: fork length relationship
Chisik Island	Juvenile	74	82.16	10.46	0.77	—
Chisik Island	Adult	205	85.26	5.86	0.90	—
Kachemak Bay	Juvenile	168	73.95	21.80	0.92	0.87
Inner-Kachemak	Adult	362	110.6	−14.30	0.88	0.84
Outer-Kachemak	Adult	481	103.7	−6.36	0.83	0.74
Barren Islands	Juvenile	101	89.40	15.90	0.87	—
Barren Islands	Adult	67	68.90	24.90	0.48	—

(Optimas) connected to a Nikon Optiphot-2 stereo microscope using 40× magnification. A consistent measurement precision (evaluated by measuring all rings on the same age-3 otolith 30 times) of $\pm 0.006 \, mm^2$ was found using this system. No significant difference was found between left and right otolith area on an initial random sample of 100 fish (paired t-test; p = 0.94). However, left otoliths were recorded throughout the investigation for consistency. More of the variation between sand lance fork-length and otolith size was accounted for by the regressions using otolith area, rather than for diameter (Table 2). We therefore used the areal measure of otolith size for analysis at all sites. In order to linearize our data, we transformed all areal measurements with a square root transformation (Zar 1984). All data analysis was done using transformed data.

Morrow (1979) and Scott (1973) have described sand lance otoliths in detail. Their basic descriptions correspond with our findings. Otoliths are basically almond shaped, the long axis is nearly straight, sulcus opens at the extreme tip and doesn't exceed 70% of the otolith length, the excisura major is present, and the excisura minor absent. However, otoliths were highly variable in finer scale details. Differing degrees to which otoliths were elongated or laterally compressed was the most obvious form of variation and probably relates to why area rather than diameter better described the otolith size/body size relationship. Other common differences included missing, wide, augmented, or forked rostrums, and a greater or lesser degree of scalloping along the otolith periphery. In 11 sand lance, one of the two otoliths (left or right) appeared decalcified with a ragged periphery and semi-translucent appearance. In none of these cases were both otoliths in this state.

Validation of opaque band formation

Adult sand lance deposit opaque material as a ring on their otoliths over a period of about 4 months in the spring (Figure 2). Duration of opaque material deposition appears to coincide with the approximately 7°C rise in water temperatures between February and June. Timing is distinctly different to juveniles, which form an opaque otolith throughout their first summer, which is subsequently referred to as the otolith core. A translucent periphery is then formed until first annulus formation the following spring. Therefore, although deposition of opaque material is an annual event, it does not precisely represent age. Core formation in juveniles (L_0), based on a January 1 hatching date (Dick & Warner 1982, Robards et al. 1999b) represents an age of 7.5 months. Opaque ring formation in adult fish ($\geq L_1$) indicates an age of $L_x + 0.25$ years where x represents age-group.

Relation of sand lance length to otolith size

A significant difference (p < 0.05; Figure 3) existed between slopes and intercepts of adult and juvenile regressions at all sites. The inner-Kachemak Bay sample had enough overlap in sizes between adults and juveniles to allow statistical comparison between adults and juveniles with the same sized otolith. Adult sand lance were significantly smaller in length (p < 0.01) than juveniles with the same sized otolith. Therefore, we used two linear regressions, rather than a single quadratic relation to describe these stocks. No significant difference in slope or intercept (p < 0.01) was found between juvenile regressions at the inner- and
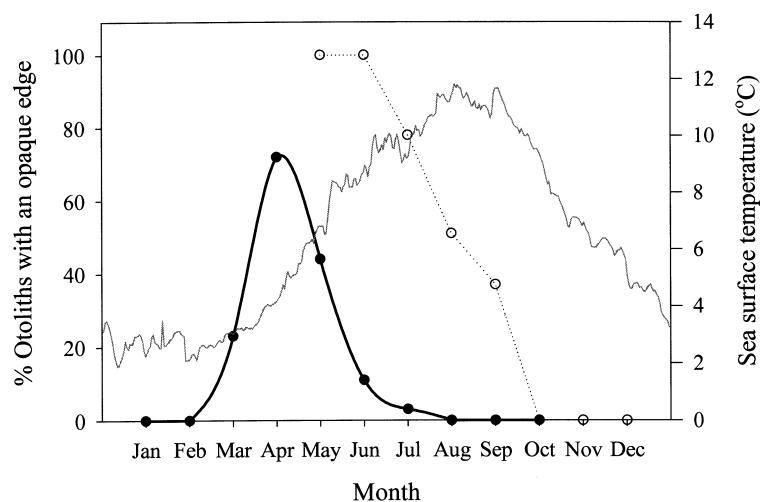
Figure 2. Seasonal proportions of otoliths with opaque edges for adult (—) and juvenile (· · ·) sand lance. The gray line depicts mean daily sea-surface temperature (SST; 1996 and 1997).
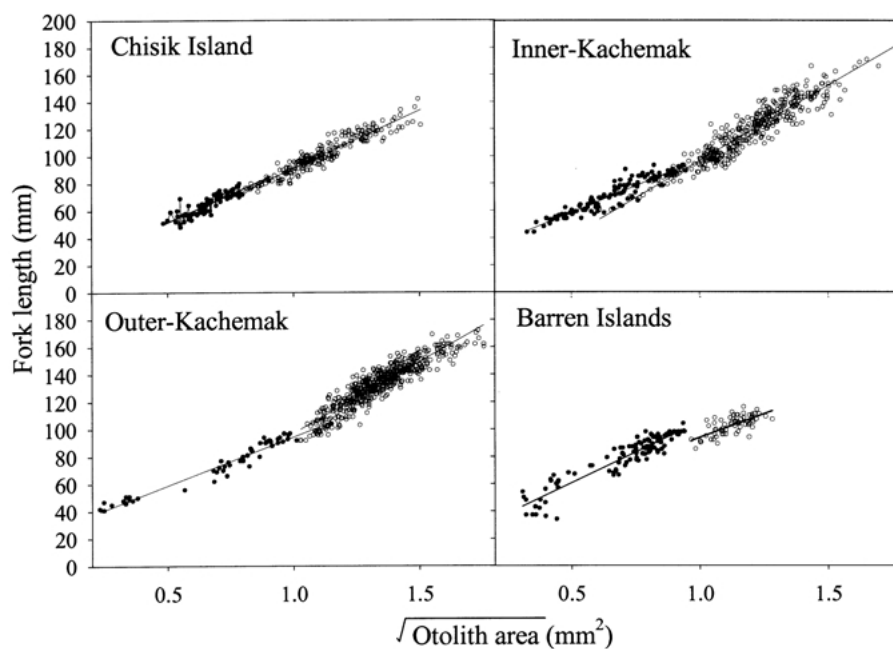

Figure 3. Relation between square root of otolith area and fork length (FL) for study sites within Lower Cook Inlet, Alaska (● = juvenile, ○ = adult).

outer-sites. Therefore, two separate regressions were produced for adults and only one for juveniles in Kachemak Bay (Table 2). Otolith area and adult sand lance fork-length at the Barren Islands was only weakly related ($r^2 = 0.48$). Regressions for juveniles were significantly different ($p < 0.01$) among the Barren Islands, Kachemak Bay (inner- and outer-bay combined), and Chisik Island. The adult relation was significantly different among all sites ($p < 0.01$). Other researchers have also described uncoupling of

somatic and otolith growth with age, and the consequent inadequacy of a single regression within the genus *Ammodytes* (e.g., Winters 1981, Wright & Bailey 1996).

Statistical analysis

Differences in the sea-surface temperature profiles for the different study areas were assessed using analysis of variance (ANOVA). Slopes and intersects of linear regressions were compared using analysis of covariance (ANCOVA). Back-calculated mean-length-at-age estimates for the different stocks were derived using the Fraser–Lee model (using separate regressions for juveniles, adults, and the different study areas). From this data we calculated growth curves using the Von Bertalanffy growth function (VBGF):

$$L_t = L_\infty \cdot (1 - \exp(-k \cdot (t - t_0))),$$

where L_t is the mean length at t years, L_∞ is the asymptotic mean length, k is a constant determining the rate of change in length increments, and t_0 is the theoretical age at zero length (Ricker 1975). Standard nonlinear optimized techniques of curve fitting were used to estimate the coefficients and their associated standard error. Due to the nonlinear formulation of the VBGF, a general linear model could not be used for analysis of covariance. Instead, an analysis of residual sum of squares was employed to compare VBGFs among areas (Chen et al. 1992).

Results

Physical environment

July sea surface temperature (SST) during 1996 and 1997 indicated significant differences among sites (ANOVA on ranks, $p < 0.01$; Table 3). There is a distinct warming of waters as they upwell at the Barren Islands and pass around the inlet via outer- and inner-Kachemak and subsequently Chisik Island (Figure 1). SSTs in 1997 displayed a similar pattern among areas, but were all warmer than those measured in 1996.

CTD profiles (Figure 4) indicated marked oceanographic differences among areas. Waters around the Barren Islands (north end of profile) were cool and well mixed. Passing through Kachemak Bay waters become increasingly stratified before circulating around to

Table 3. Mean July SSTs for 1996 and 1997 at Chisik Island, inner and outer Kachemak Bay, and the Barren Islands.

Location	1996		1997	
	Mean	sd	Mean	sd
Chisik Island	10.6	0.5	11.5	0.5
Inner-Kachemak	9.7	0.7	10.1	0.5
Outer-Kachemak	9.1	0.7	9.4	0.6
Barren Islands	8.5	0.6	8.6	1.1

Chisik Island (west end of profile) where waters are warm, low salinity, and weakly stratified.

Catch

No adult sand lance were caught by beach seine during winter months (November–March) and were only found in exposed intertidal sediments during this time period. Juvenile sand lance were dominant in the nearshore from late June into winter (Robards et al. 1999a). To assess relative abundance among areas, frequency of capture, catch-per-unit-effort (CPUE), and median catch were calculated for July and August (Figure 5). Sand lance at Chisik Island were caught about one third the frequency and in fewest numbers compared to the other sites. Frequency of juvenile capture and sand lance abundance were greater for inner-Kachemak Bay compared to the outer-bay. Catches at the Barren Islands were an order of magnitude greater than the other sites. However, most catches at this site were exclusively juveniles or mixed with low numbers of adults.

Inter-seasonal growth

Slopes and intercepts of length–weight regressions ($\log_{10}$ transformed; Table 4) were significantly different (ANCOVA; $p < 0.01$) from zero. Regression slopes and intercepts were also significantly different among areas ($p < 0.01$). The regression slope was highest at the Barren Islands suggesting that the condition of juveniles was greatest at this area (greatest weight per unit length). A significant ($p < 0.01$) difference also existed between the spring and fall relation for sand lance in inner-Kachemak Bay, with fall sand lance displaying greatest weight-per-unit-length.

A total of 3909 otoliths were used to produce age/length keys for the different sites (Table 1). Juvenile sand lance grow rapidly from at least May
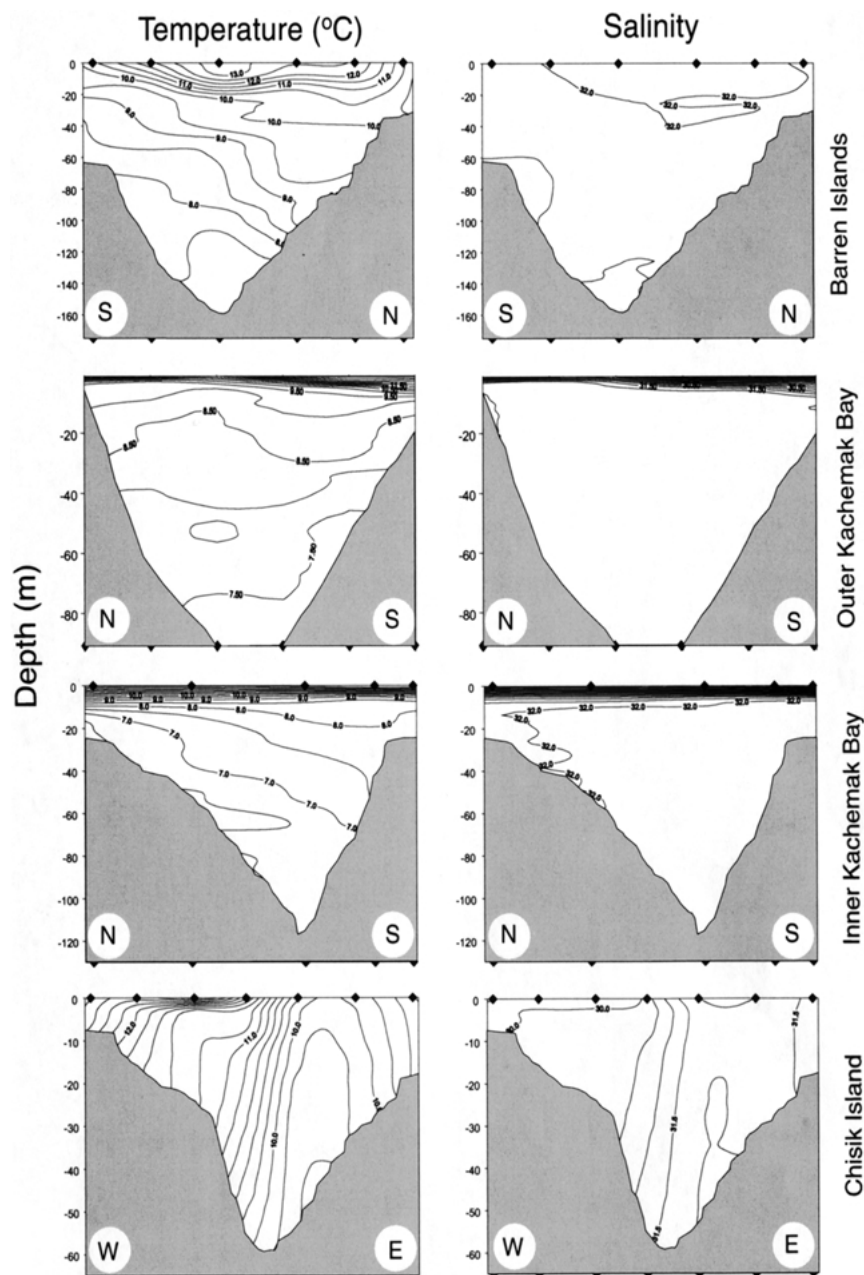
Figure 4. Temperature and salinity profiles for transects in Lower Cook Inlet at the Barren Islands, inner- and outer-Kachemak Bay, and Chisik Island. Transect locations are depicted in Figure 1 with the compass direction given at the base of each profile.

when they recruit to the nearshore until September (Figure 6). During this period juveniles increased in size by 100% and 110% during 1996 and 1997, respectively. This corresponds to about 88% of total annual growth, in contrast to the 12% of annual growth observed in the subsequent 7 months. Adult sand lance grow over the same period, but to a lesser degree. Growth decreased with age during the May–September period, with an average 30%, 8%, and 3% increase observed in age groups 1, 2, and 3, respectively. For
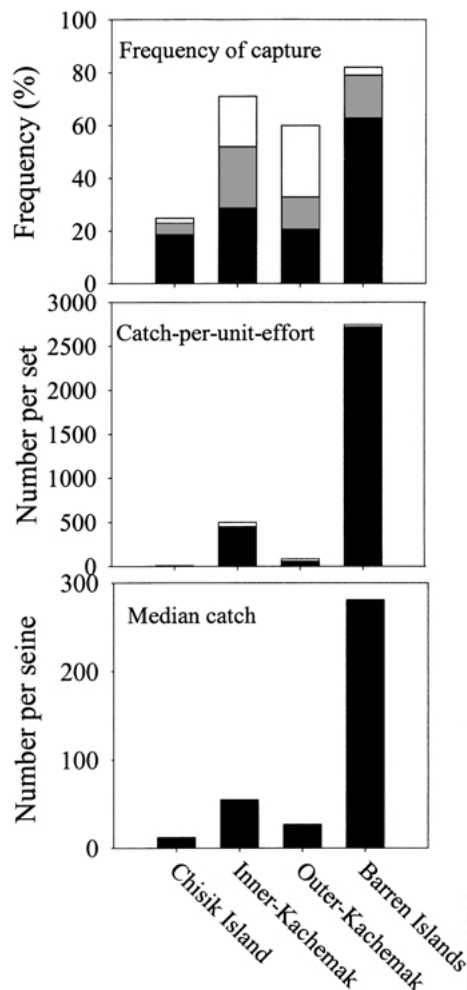
Figure 5. Indices of catch and abundance from beach seine data collected at Chisik Island, inner- and outer-Kachemak Bay, and the Barren Islands during June–September 1996 and 1997; ■ = juveniles, ▨ = mixed adults and juveniles, □ = adults. Median catches are for combined adult and juvenile data.

Table 4. Relationship between length and weight for sand lance collected at the different sites in 1996 and 1997. Two seasonally different regressions are given for inner-Kachemak. Relationship is expressed as: $\text{Log}_{10}(\text{weight [g]}) = (a \cdot \text{Log}_{10}\text{fork length [mm]}) + b$.

Location	Season	n	a	b	r^2
Chisik Island	July/August	681	3.28	−6.02	0.99
Inner-Kachemak	July/August	5192	3.25	−5.95	0.99
Inner-Kachemak	May/June	1210	2.98	−5.50	0.99
Outer-Kachemak	July/August	1487	3.20	−5.87	0.99
Barren Islands	July/August	3799	3.48	−6.40	0.98

Table 5. Von Bertalanffy parameters and (standard error) for the study sites.

Parameter	Chisik Island	Inner-Kachemak	Outer-Kachemak
L_{inf} (mm)	135.61 (3.81)	235.74 (18.1)	166.33 (1.61)
K	0.3718 (0.04)	0.1528 (0.02)	0.4798 (0.02)
t_0	−1.7094 (0.17)	−2.8252 (0.30)	−1.5143 (0.07)

calculation). Size of sand lance in Kachemak Bay was more variable than the Barren Islands.

Interannual growth

No VBGF data was calculated for the Barren Islands as only two age-groups (0 and 1) were represented. Most variability was found for the inner-Kachemak sample (Table 5). Fish from the nearshore areas around Chisik Island initially grow more slowly as evidenced by length at age-0, and ultimately reach a smaller size than for any other areas within the investigation (Figure 7). Although sand lance from inner- and outer-Kachemak Bay were similar in size at the end of their first growing season, sand lance from the outer-bay subsequently grew faster than those from the inner bay. Significant differences (p < 0.01) were observed between Von Bertalanffy growth curves at Chisik Island and inner-Kachemak Bay (F = 222, df = 13.7), Chisik Island and outer-Kachemak Bay (F = 1296, df = 13.7), and between inner- and outer-Kachemak Bay samples (F = 22, df = 14.8).

Assessment of Lee's phenomenon

Lee's phenomenon can indicate selection against larger individuals in subsequent year classes. The

age-group 3 adults, this constituted 100% of their annual growth for the 1996/1997-time period. Concurrent increases in variability of mean length with age due to small catches prevented accurate assessment for older age-classes.

Sufficient catches of juveniles from inner-Kachemak Bay and at the Barren Islands allowed us to produce time-series data for both 1996 and 1997. Growth in 1997 was slightly faster than 1996 for both sites based on regressions plotted between June and September (Figure 6). After September, growth markedly slows (post-September data are not included in the regression
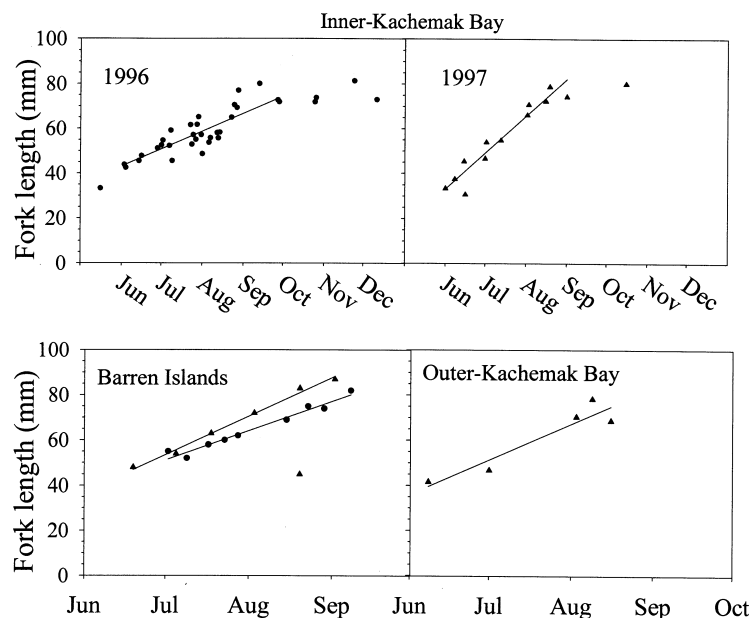
Figure 6. Seasonal growth of juvenile sand lance collected by seine from inner-Kachemak Bay and the Barren Islands during 1996 (●) and 1997 (▲), and outer-Kachemak Bay during 1997. Plots are derived from mean juvenile size in daily catches. Growth rates for the June–September period in 1996 and 1997 respectively of 0.43 ($r^2 = 0.97$) and 0.57 mm day^{-1} ($r^2 = 0.99$) at the Barren Islands, and 0.27 ($r^2 = 0.62$) and 0.53 mm day^{-1} ($r^2 = 0.91$) at inner-Kachemak Bay were observed. Growth rate for 1997 in outer-Kachemak Bay was 0.53 mm day^{-1} ($r^2 = 0.89$). The small-sized cohort of sand lance that passed through the Barren Islands in 1996 was an anomaly and not included in the regression calculation.

phenomenon was clearly apparent for sand lance collected from Chisik Island, but not for the Kachemak Bay sites (Figure 8). As the same non-selective sampling strategy was used at all sites, maturity stages were treated separately, and Chisik Island sand lance were all collected from the same beach, we expect that this phenomenon is real as opposed to an artifact of the Fraser–Lee method of back-calculation. The occurrence of only two age-classes at the Barren Islands prevented a relation being observed at this site.

Discussion

Similar to the findings of Winters (1981) for the northern sand lance, *A. dubius*, we found that within stocks (between years) growth rates were positively correlated with temperature. However, in contrast to Winters (1981), this relationship did not exist in inter-location comparisons. Sand lance from Chisik Island, where waters were warmest, were smallest and grew slowest while, juveniles from the Barren Islands, where waters were coldest, grew fastest.
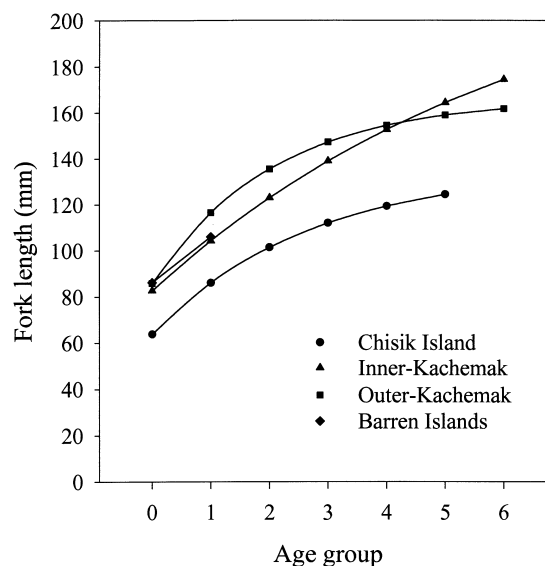

Figure 7. Von-Bertalanffy growth curves fitted to back-calculated length-at-age data for Chisik Island, Inner-Kachemak, and Outer-Kachemak. No growth curve was calculated for the two age-classes present at the Barren Islands; actual size at age values have been added to the graphic for comparison.
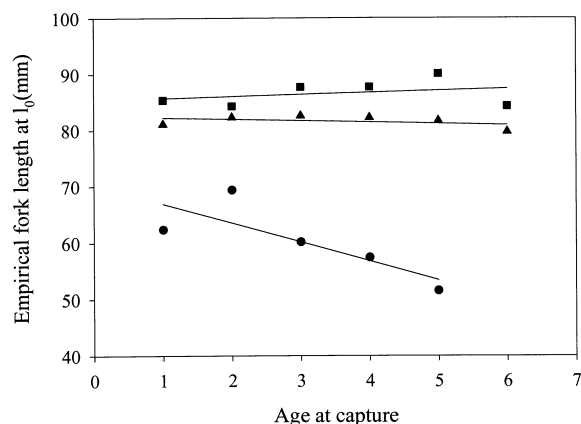
Figure 8. Graphical assessment of Lee's phenomenon using the relation between back-calculated length at the end of the first growing season (l_0) and age (■ = outer-Kachemak Bay, ▲ = inner-Kachemak Bay, ● = Chisik Island).

A. hexapterus appears typical of the genus (e.g., *A. marinus*, Brêthes et al. 1992, *A. personatus*, Kitakata 1957); growth is primarily associated with the spring and summer when 80–100% of annual growth occurs. Warmer temperatures in Kachemak Bay and at the Barren Islands in 1997 compared to 1996 were reflected in faster growth of juvenile sand lance. However, these differences were not as profound as the growth differences observed among stocks. Furthermore, differences among sites were negatively correlated with temperature and positively correlated to productivity. We suggest that productivity and the resultant food (zooplankton) availability may be the dominant factor regulating growth. Macer (1966) also suggested that differences in growth for *A. marinus* on different offshore banks were attributable to site-specific current regimes supplying different densities of food. Changes in food availability can beproduction-related or a result of density dependence. Unequivocal and profound production differences exist between our study areas and can alone be correlated with the differences in growth that we observed. Productivity at Chisik Island is considerably less than in Kachemak Bay (Damkaer 1977, Larrance et al. 1977, Drew[1]) and is reflected in poorest sand lance growth of all sites. Faster growth of adult sand lance in the cooler outer-Kachemak Bay compared to the inner-bay suggests food may be more limited in the inner-bay.

[1] Gary Drew, U.S.G.S. Biological Resources Division. Unpublished zooplankton abundance data from 1996 and 1997.

Currents entering outer-Kachemak Bay are upwelled-highly productive oceanic waters, which subsequently become increasingly depleted as water passes around the inner-bay during the summer (Larrance et al. 1977). Further evidence of plentiful zooplankton in outer-Kachemak Bay is that this area supports the greatest epifaunal biomasses found in Cook Inlet (Feder & Jewett 1987). The Barren Islands are surrounded in nutrient rich waters as they upwell from the Gulf of Alaska into lower Cook Inlet. Damkaer (1977) indicated that the persistent upwelling resulted in a lengthened period of summer productivity in this region. Resultant food abundance is probably the reason for the fastest growing and highest condition sand lance within the inlet.

Although production-related food availability can account for the growth differences in lower Cook Inlet, density dependence may exacerbate these effects at the two Kachemak Bay sites and Chisik Island. Damkaer (1977) described a small bloom in the Chisik area in late summer (July). In contrast a large spring (May) bloom exists in Kachemak Bay. Although sand lance at Chisik Island are at low abundance, the later bloom may increase intraspecific competition. Juveniles and adults that are largely segregated during the spring bloom in Kachemak Bay (pre-recruitment to nearshore; Robards et al. 1999a), are present concurrently in nearshore Chisik Island waters and competing for similar prey during July (Field 1988). Greater abundance of sand lance in inner-Kachemak Bay (particularly juveniles) compared to the outer-bay may also increase competition at this site. This may contribute to adults growing faster in the outer-bay, despite being of equal size at the end of their first season. Numerous density-dependent effects between maturity stages of sand lance have been reported for the Japanese sand lance, *A. personatus*, including increased mortality and reduced growth (Field 1988).

Whereas temperature, production patterns, and density issues are correlatedwith sand lance growth, habitat is critical to abundance. Juvenile sand lance from the-Barren Islands had a greater weight to length ratio and grew fastest despite being in far greater numbers than at the other sites, suggesting plentiful food. Therefore, low numbers of adults at the Barren Islands compared to the Kachemak Bay sites is probably attributable to habitat requirements rather than food or density issues. Although sandy beaches are evident around the islands, few of these beaches are sheltered, and all are subject to regular onshore wave action. The perpetual winter

storms that plague the Barren Islands would result in constant disturbance of these substrates and preclude the normal sustained winter dormancy (Field 1988) at a time of low food availability. In a similar fashion, outer-Kachemak Bay is much more exposed to onshore wave action than the inner-bay. This may explain the lower sand lance abundance in outer-Kachemak Bay. Sediment laden waters around Chisik Island (Feely & Massoth 1982) render most nearshore areas muddy. This type of substrate is generally unsuitable for sand lance (Pinto et al. 1984), and probably accounts for the lowest observed abundance of sand lance at these Cook Inlet locations.

In addition to the oceanographic consequences to growth and abundance of sand lance at Chisik Island, selection against larger individuals may also exist. The occurrence of Lee's phenomenon suggests that there is either size selective sampling or that there is size selective mortality of larger fish within the stock. As beach seines are regarded as non-size selective (Cailliet et al. 1986), we treated sand lance stocks and maturity stages separately, and as we did not observe this phenomenon in Kachemak Bay, we concluded that larger fish within cohorts at Chisik Island are exposed to higher mortality, as opposed to this being a methodological bias. Lee's phenomenon has also been described for sand lance (*A. dubius*) collected in the North Atlantic (Winters 1981), and attributed to discriminatory mortality of the faster growing (earlier maturing) individuals. The high energetic requirements required for gaining full maturation (Robards et al. 1999b), poorer condition, and the immediate onset of winter with limited food availability (Damkaer 1977) might result in larger sand lance at Chisik Island entering winter with insufficient reserves. Winters (1974) showed Lee's phenomenon for capelin, *Mallotus villosus*, and also suggested higher spawning mortality for larger, faster-growing individuals of this species. Otoliths in adult sand lance stocks at Chisik Island were relatively large compared to similar sized individuals from Kachemak Bay. Relatively large otoliths within slow-growing individuals are quite common in fish stocks such as at Chisik Island due to systematic variation in the somatic-otolith size relation with changes in somatic growth (Ralston 1995).

Finally, Chisik Island sand lance are smaller at age than those in Kachemak Bay. As fecundity is directly proportional to size (Robards et al. 1999b), smaller fish contain lower number of eggs. Therefore, productivity may be compromised and be partially responsible for the lower numbers of sand lance found at this site.

Our site-specific results, coupled with minimal migrations (Hobson 1986) and localized spawning (Robards et al. 1999b) by this species, suggest that adult *A. hexapterus*, as for Atlantic sand lance, *A. dubius* and *A. americanus* (Scott 1972), exist in distinct stocks with specific growth parameters, demonstrate site fidelity, and are generally limited in movement along coastlines. The ecological implications of site fidelity may be catastrophic if nearshore sand lance habitat is rendered unsuitable from anthropogenic perturbations such as oiling (Pinto et al. 1984).

Implications to predators

Among-site differences in sand lance abundance, seasonal growth, size-at-age and mortality reflected differences in oceanography among sites. In turn, this geographic variability in sand lance availability and quality has important implications for the numerous sand lance predators that reside in each area. Each of the study areas supports important stocks of marine piscivores such as cetaceans, pinnipeds, and seabirds. Perhaps the most important issue to these predators regarding sand lance is the large differences in abundance among sites. Predators are presented with a profoundly lower abundance of sand lance around Chisik Island. For some predators this may lead them to switch to a more abundant species (if available), and for others may lead to increased search time and range to acquire sufficient prey. Furthermore, the sand lance that they collect from nearshore areas around Chisik Island are likely to be of smaller size than in Kachemak Bay. This may be particularly important to certain species such as seabirds that are returning prey (sometimes singly) to their chicks.

Implications in trophic energy flow analysis

The consequences of differing growth and otolith relationships among sites can have profound implications to estimates of trophic energy flow. Otolith-somatic size regressions are frequently used to back-calculate size of prey in diet studies. Frequently, these calculations use a single regression (Campana 1990). The potential error of using a single regression can be demonstrated using a single pooled Lower Cook Inlet otolith dataset. A 120 mm sand lance collected at Chisik would be estimated as approximately 5 mm larger than

when back-calculated from a locally derived regression. Although only a 4% difference in length, the difference would translate to an increase in mass of 0.9 g, equivalent to an energy density (ED) difference of as much as 5.7 kJ (14%; ED value from Anthony & Roby 2000). This discrepancy is similar to seasonal ED adjustments used by Mårtensson et al. (1996), who indicated a 10–15% difference in ED could amount to as much as 300 000 tonnes of prey during the feeding season for minke whales. As sand lance of the same species frequently show great disparity in growth among neighboring regions (e.g., Scott 1973, Dick & Warner 1982, this study) the significance of identifying the geographical source of prey for predator foraging studies is obvious.

Acknowledgements

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